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**Forest Structure and Intraspecific Positional Behavior Variation in *Alouatta palliata***

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**Abstract**

The relationship between forest structure and positional behavior is examined in the mantled howling monkey (*Alouatta palliata*) in primary and secondary rainforest habitats in northeastern Costa Rica. Despite structural differences between the two study sites, there are no significant differences in habitat use or positional behavior frequencies. Overall, the mantled howler monkey locomotor repertoire is centered on quadrupedalism and bridging, with sitting and suspension as predominant feeding postures. Howlers prefer small and medium horizontal supports, and use the upper and lower canopy frequently. Several methodological factors may have limited the results and analysis of this study. Temporally, the study was limited to the wet season, which may have implications for positional variability. A lack of distinction between travelling and foraging behaviors may have influenced the data. The study sites may also not have been distinctive enough to accurately reflect the influence of forest structure on positional behavior. The results were similar to those of a number of other studies of *A. palliata*, and are comparable with the positional behavior of the species and the genus as a whole. Without data from a more diverse array of mantled howler habitats, it is difficult to analyze site-specific intraspecific variation through cross-study comparisons. Previous discussions of intraspecific positional behavior variation in *A. palliata* have relied on cross-study comparisons, which can be problematic. Ultimately, the relative resilience of howlers to anthropogenic disturbance has been noted for some time, and the possible positive implications of this study are discussed. Further standardized research is necessary to fully examine intraspecific positional behavior variation.

## 1. Introduction

The purpose of this thesis is to analyze the influence of habitat type and structure on the positional behavior of the mantled howler monkey (*Alouatta palliata*). The anthropological relevance of this thesis is twofold. Studies of positional behavior of modern primates, in conjunction with the study of their anatomy, are crucial to reconstructing the behavior of extinct primate species. These studies reflect an important part of the behavioral ecology of primates, and in turn are useful for conservation activities, as an understanding of habitat usage is integral to conserving and restoring habitat that can be used by impacted species. This thesis is based on research in two distinct primary and secondary rainforest habitats conducted over an eight-day period at La Suerte Biological Research Station, in northeastern Costa Rica.

The story of the primate adaptive radiation, and particularly of primate positional behavior, is one of extraordinary diversity. A thorough understanding of adaptive diversity among the order Primates is highly dependent upon the study of positional behavior, and the traits that are closely related to it, such as habitat usage and evolutionary locomotive and postural adaptations. Positional behavior as we know it today refers to a combination of locomotor and postural behavior (Prost, 1965). Traditional locomotor behavior studies might analyze usage rates of movement behaviors, such as leaping versus running, or details of specific locomotive acts, such as the distance and method of leaps. Positional behavior incorporates postures into the equation, in addition to movement, such as sitting versus clinging. These data are useful in several regards. Through analysis of the positional behavior of extant primate species, it is possible to reconstruct the behavior of closely related or morphologically similar extinct species as accurately as possible. These studies are also integral to understanding primate evolution itself, as a species' adaptation is closely linked to its ability to use the environment, escape

predation, and access food resources. Though less widely explored, these studies have important implications for primate conservation as well.

From its origin, the primate lineage has been primarily one of arboreal habitat use. Among the earliest primates and their descendants, a variety of traits associated with such a behavior pattern are visible. Grasping feet with opposable big toes and flattened nails proved useful for climbing and grasping surfaces such as tree limbs, as did forward facing eyes due to orbital convergence, which allow for greater depth perception. Color vision allowed these early primates to distinguish between more and less desirable arboreal food sources, such as young versus old leaves, or ripe versus immature fruits (Garber, 2007). In more recent periods of primate evolution, positional morphology in primate species has diversified significantly. Derived traits such as the evolution of claw-like nails in tamarin and marmoset (subfamily Callitrichinae) species (after the evolution of flat nails in place of claws initially within the primate order), prehensile and semi-prehensile tails within several species of New World monkeys, including howler and spider monkeys (family Atelidae) and capuchins (family Cebidae), respectively; and the emergence of bipedal locomotion among early hominid species are some of the more obvious examples of this diversity. These morphological adaptations are integral to the behavioral repertoires of their respective species, and the wide geographical and behavior range of extant primate species is dependent upon them. As Jolly and Plog have stated, “almost every major adaptive radiation within the primate order has involved changes in locomotor patterns that opened up a new array of niches” (qtd. in Garber, 2007: 544).

Cant (1992) provides a useful framework for understanding the significance of variation in positional behavior and morphology: specifically, it provides a method of examining the relationship between morphology and natural selection. Positional behavior allows individuals

to solve three distinct problems associated with habitat: food acquisition, predator avoidance, and habitat navigation. Particularly among arboreal primates, these three problems are all largely related to habitat type and structure. Arboreal habitats can be difficult to navigate: tree limbs exist in a wide variety of sizes and orientations, and animals must frequently use small terminal ends of branches to attain desirable food resources or cross gaps between trees. To Cant, positional behavior allows arboreal primates to straighten the path of movement and increase speed along that path, use large vertical supports (tree trunks), cross gaps between trees, access food resources on thin supports, and acquire mobile prey. Research by Cannon and Leighton (1994) has indicated that gap crossing and efficient and direct movement paths strongly constrain positional behavior among Bornean agile gibbons and long-tailed macaques. Behaviors used for food acquisition, predator avoidance, and habitat navigation are largely similar due to their close relation to habitat structure, despite the differences in motive behind them (Cant, 1992). Through these behaviors, primates can avoid predators and access food, positively impacting their chances to reproduce.

Despite their increasing frequency, comparisons of positional behavior studies are difficult, as definitions of postures and other variables can vary widely among researchers. Despite attempts to rectify this problem by establishing a list of standardized descriptions of variables (Hunt et al., 1996), it remains relatively common due to historical precedents to use undefined or poorly defined terms, and unique variables invented for specific cases. Despite these issues, between-species comparisons of positional behavior within similar habitats or among closely related species have been a successful field of research.

Often, these comparisons focus on sympatric species, as in a seminal work by Fleagle and Mittermeier (1980) in central Surinam. Analyzing the positional behavior of seven monkey

species (golden-handed tamarins, squirrel monkeys, white-faced sakis, bearded sakis, tufted capuchins, red howlers, and black spider monkeys), Fleagle and Mittermeier concluded that positional behavior is closely related to body size, resulting in the long held maxim that as body size increases, climbing increases and leaping decreases. These researchers also noted that leaping tended to occur in the understory level and in liane forests, while other locomotor modes were associated with the main canopy level. Another study of six sympatric species in Ecuador attained similar results (Youlatos, 1999).

More recent studies by McGraw (1998a, 2000) and Gebo and Chapman (1995b) have challenged these ideas. Studying six sympatric Old World species (in contrast to Fleagle and Mittermeier's (1980) New World primates), McGraw found that body size does not predict leaping or climbing frequencies, and in fact that climbing tended to be associated with foraging behavior, in which individuals move and feed around a centralized area without overall group direction, and travelling behavior, in which individuals tend to move as a group from point to point (1998a). Gebo and Chapman, studying five sympatric species in the Kibale Forest of Uganda, attained similar results (1995b). In addition, larger support use was associated with travelling, while smaller supports were used for foraging, congruent with Cant's (1992) observation that food resources tended to be located on smaller supports, often at the terminal end (McGraw, 1998a). These observations regarding travelling versus foraging are indicative of another common problem in comparisons of positional behavior studies: often, particularly in older works, travelling and foraging are not distinguished between, and are instead grouped together as general movement behavior.

Over the past twenty years, studies of intraspecific (within-species) positional behavior have become more common, though the field remains under-researched and often confounding.

Intraspecific variation may be seen or expected between sexes, due to differences in body size, social roles, and reproductive costs; along age classes, due to developmental changes along both biological and social lines; and along seasonal and site-specific lines, due to differences in habitat structure (Garber, 2007; Bezanson, 2006, 2009). Several factors, such as the significant sexual dimorphism present in many primate species, suggest that sex-based intraspecific positional behavior variation would be common. Generally, this does not appear to be the case. In several studies of chimpanzees (*Pan troglodytes*), gorillas (*Gorilla gorilla gorilla*), and orangutans (*Pongo pygmaeus*), any intraspecific variation present at all has been extremely subtle, despite sex-based size differences ranging from 30 to 220% by species (Garber, 2007). Studies of both Old and New World monkeys have attained similar results (Gebo and Chapman, 1995b; Gebo, 1992; Wheeler and Ungar, 2001). Among age-classes, intraspecific variation appears to be more pronounced (Bezanson, 2006, 2009). In a study of positional behavior of white-faced capuchins (*Cebus capucinus*) and mantled howler monkeys (*Alouatta palliata*), the two species displayed different patterns of positional behavior as they matured, in which *Cebus* individuals attained an adult behavioral pattern within 6 months, while *Alouatta* locomotion differed from the adult pattern for 24 months (Bezanson 2009). Bezanson suggests that these differences may relate to differing environmental pressures on developing *Alouatta* and *Cebus*.

Studies of seasonal and site-specific positional behavior variation have seen mixed results. Gebo and Chapman (1995a), studying the positional behavior of the red colobus monkey (*Colobus badius*) across several seasons and habitat types in the Kibale Forest of Uganda, found a remarkable degree of behavioral variance. Research was conducted within three distinct areas of the forest with differing logging histories: a primary forest, secondary forest, and pine plantation. In each of these habitat types, the habitat structure differed in percentage of



continuous canopy, distance between trees, and sizes and frequencies of canopy gaps. In addition, observations continued through two dry seasons and one wet season in the primary forest area. In general, year to year variation was more significant than any seasonal variation. Some seasonal variation, particularly during foraging, was more pronounced: during the wet season, quadrupedalism decreased by 21%, while climbing and leaping increased by 9% and 8%, respectively. This variation was likely related to seasonal differences in food distribution in the canopy (Youlatos 1998). Between habitat types, dramatic variance was observed in foraging behaviors, and travelling behavior was more conservative. Support use also differed among habitat types and along seasonal lines. Despite this variation, the authors note that “common behaviors remain common, and thus, radical changes in positional behavior do not occur in different ecological contexts,” though “clearly, primates are more flexible in their behavioral adjustments to different ecological settings than previous work has documented” (Gebo and Chapman, 1995a).

A similar study undertaken by Garber and Pruetz (1995) of moustached tamarins (*Sanguinus mystax*) in two distinct research sites in Peru revealed significantly less positional behavior variation. The authors collected data in relatively undisturbed primary and secondary rainforest at the Rio Blanco field site and in a highly disturbed forest area “dominated by low secondary growth, planted orchards and open grassy fields” at the Padre Isla field site (Garber and Pruetz, 1995: 412). Despite these extreme differences in forest structure, positional behavior variation was nearly nonexistent. Further research by Garber (1998) at the same sites has supported these conclusions, noting only minor differences in positional behavior and diet between sites. It is worth noting that in a separate study of interspecific variation among three tamarin (*Sanguinus spp.*) species, including *Sanguinus mystax*, Garber found little evidence of

significant variation in positional behavior (Garber, 1991). It is possible that the relatively small size of tamarins may preclude the need of the animals to adapt to distinct habitat types through behavioral variation.

A study of diademed sifaka (*Propithecus diadema edwardsi*), brown lemur (*Eulemur fulvus rufus*), and red-bellied lemur (*Eulemur rubriventer*) populations in two sites in Ranomafana National Park in Madagascar also provides a useful example of intraspecific variation, and the challenges facing studies of the same (Dagosto and Yamashita, 1998). The authors noted differences in canopy use, support use, and positional behavior between the two sites, as the lemurs used larger, taller trees, stayed higher in those trees, leaped less and climbed and moved quadrupedally more in the site with significantly taller and larger trees. These differences are likely related to a significant difference in travelling versus foraging behavior recorded at the two sites. Due to the noted difference in positional behavior during foraging and travelling, the Dagosto and Yamashita's results may be skewed. The authors do point out, however, that the variation recorded is more dramatic than would be expected due to travelling versus foraging alone.

Howler monkeys (*Alouatta spp.*) are a wide ranging, resilient, and successful genus of platyrrhine primates (New World monkeys). The taxa are notable for a number of characteristics, such as a high degree of folivory (in comparison to other highly frugivorous New World monkeys), prehensile tails (unique to the family Atelidae), a slow, deliberate style of arboreal quadrupedal locomotion, the tendency to rest for upwards of half of each day, and of course for the howling vocalizations that give the genus its common name (Bezanson, 2006; Prates and Bicca-Marques, 2008). Howlers use a slow method of quadrupedal walking for most

locomotion, generally sit when feeding, and rest throughout much of the day, especially after feeding periods (Prates and Bicca-Marques, 2008).

Howlers are known for their resiliency and ability to adapt to degraded and fragmented environments with a relatively great deal of success. This trait is likely related to a degree of flexibility in diet and activity patterns within the genus. In a study at Los Tuxlas, in Veracruz, Mexico, Cristóbal-Azkarate and Arroyo-Rodríguez (2007) reported that the size of a forest fragment has little effect on most aspects of howler behavior and ecology, but that population density within fragments was a good predictor of howler ecology. As population densities increase, the amount of plant species utilized for food increases, as does the amount of consumption of plant items other than fruits, leaves, and flowers, such as bark and lianas. This diversification of diet may be important to the resiliency of the genus. In Cristóbal-Azkarate and Arroyo-Rodríguez's (2007) study, secondary food items such as bark and lianas were not consumed often, but were eaten in large quantities when they were utilized, suggesting that they may be used as primary food sources when more desirable foods are not available. Oddly, consumption of fruit, leaves, and flowers did not seem to be affected by population density within forest fragments. Leaves, which are relatively low in quality but high in abundance, could be utilized more heavily when high quality food resources like fruit and flowers are unavailable, but this does not seem to be the case. Cristóbal-Azkarate and Arroyo-Rodríguez (2007) also noted that home range sizes decreased as fragment sizes decreased. This was likely accomplished through the consumption of secondary food sources, allowing groups of howlers to subsist on smaller habitat areas. Despite this resilience, there are a number of dangers associated with habitat fragmentation and degradation.

Forest fragmentation is often the outcome of anthropogenic activities, such as farming and ranching. As fragmentation occurs, continuous forest landscapes are gradually transformed into collections of small forest patches surrounded by artificially modified land. This modified land can range from pastures for cattle grazing, in which there is a clear division of forest and non-forest environments, to regenerating forest habitats that were at some point in the past logged either selectively or completely, to orchard forests, in which the natural structure of a forest gives way to agricultural lands that are in some way integrated with the forest fragment (Arroyo-Rodríguez and Dias, 2009). After fragmentation, there are a number of factors, both natural and anthropogenic, that can endanger howler populations living within fragments. Depending on location, poaching for the pet trade and hunting for meat can be particularly dangerous for howlers in fragments (Arroyo-Rodríguez and Dias, 2009). When howlers are confined to small patches, human hunters and poachers can access the animals more easily. Luckily, in many areas, this threat is low, as howlers are not valued as pets or as food as many other primate species are (Arroyo-Rodríguez and Dias, 2009). In some cases, howlers are forced to travel from one isolated fragment to another, typically by terrestrial locomotion. This can be problematic, exposing howlers to natural predators such as jaguars and coyotes and human-introduced predators such as dogs (Arroyo-Rodríguez and Dias, 2009). Several less explicit threats can also affect howlers living in patches, such as a loss of genetic diversity over time, as individuals are unable to either leave or enter a patch, and social conflict, as individuals reaching maturity are unable to disperse from their groups (Arroyo-Rodríguez and Dias, 2009).

Howler monkey positional behavior is best described as deliberate arboreal quadrupedalism. Mendel described the locomotion of mantled howlers as “almost invariably slow and deliberate, the prehensile tail providing a secure support during nearly all locomotor

activities” (Mendel, 1976: 44). Climbing is also a common locomotor mode (Gebo, 1992).

Despite their occasional classification as semi-brachiators, brachiation is not a locomotion used by howlers, unlike closely related species such as spider monkeys (*Ateles spp.*), precluding the possibility of gap crossing through brachiating swings (Mendel, 1976). When crossing gaps in the forest canopy, howlers perform one of two actions: leaping or bridging. Bridging, a procedure in which an individual uses its hands to grasp a new support while holding on to another support with its back feet and tail, is more common than leaping, and in some cases is one of the more common elements of the howler positional repertoire (Gebo, 1992). Bridging is associated with the slow quadrupedalism used by howlers, as well as their large body size, and may allow howlers to transform the potential energy of slender supports into kinetic energy in order to help them cross gaps, explaining the prominence of the behavior over leaping (Youlatos, 1993).

During feeding behavior, howlers tend to use a combination of tail-assisted suspension and sitting postures. Young leaves—one of the preferred food resources of howlers—tend to be located on the terminal ends of supports, which are often thin and flexible. As such, tail and hindlimb suspension are often used to access these resources, as suspension allows the animals to reach further while freeing their hands to access food. In addition, through suspension, howlers can avoid the trouble of attempting to balance on thin and flexible supports (Mendel 1976). Research by Wheeler and Ungar (2001) has indicated that tail use is associated with feeding and is rarely used during traveling; also, tail use is most common on small, horizontal or oblique supports. The tail is often wrapped around supports while the animals rest as well, providing additional support (Mendel 1976).

Variation in habitat use by howlers tends to be fairly conservative, although differences between sexes have been noted. Howlers typically use the upper canopy more than any other forest level, and prefer small to medium horizontal and oblique supports (Mendel 1976). Gebo (1992) reported that females tended to use smaller supports and the lower canopy more often than larger males, possibly because their smaller size allows them to use a wider range of supports than males. During foraging behavior, smaller oblique supports are used more than in traveling, in which larger horizontal supports are preferred, likely as a result of easing the navigation of the forest structure.

The mantled howler monkey is a highly successful species, capable of thriving in a variety of habitats in various states of forest degradation. This diversity makes them a good candidate for an analysis of positional behavior differences between habitat types. Comparing mantled howler monkey populations in two distinct forest habitats at La Suerte Biological Field Station in northeastern Costa Rica, I predicted that the positional behavior and habitat usage of the animals would vary between the two habitat types. I predicted that suspensory postures and small supports would be used more often in secondary forest environments, due to the smaller overall tree sizes. I also predicted that gap crossing behaviors such as leaping and bridging would be more common in secondary forest habitat, due to the lack of continuous canopy in comparison to primary forest.

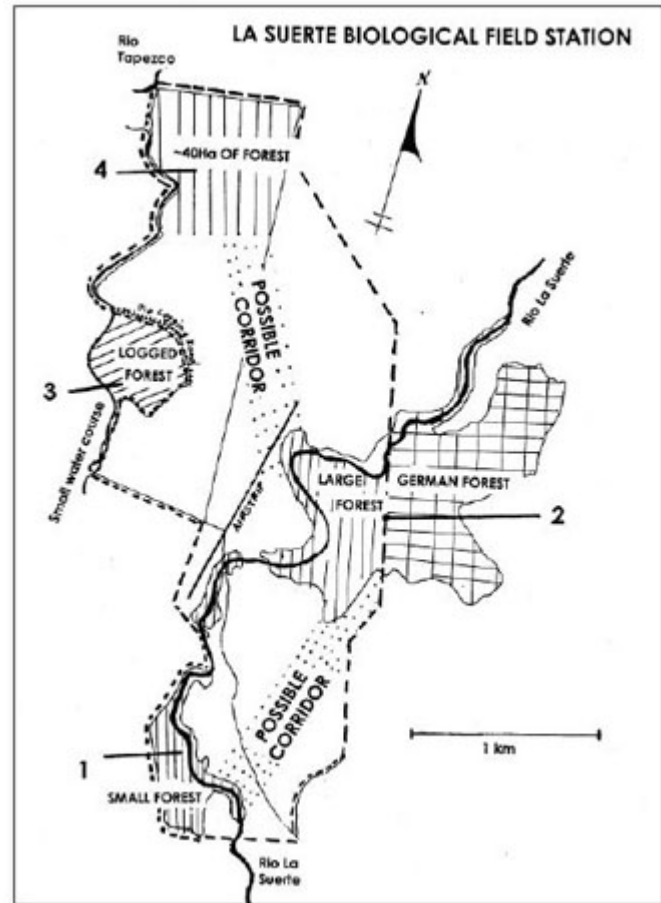
## **2. Methods**

Research was conducted in 2010 at La Suerte Biological Research Station (LSBRS) in northeastern Costa Rica, approximately 20 km from the Atlantic coast. The research station, purchased by the Molina family in 1987, is approximately 250 ha in size, and is comprised of primary and advanced secondary lowland tropical rainforest, as well as areas that were

selectively logged in the 1970s (Garber and Rehg, 1999; Slocum, 2001; Bezanson, 2006). The majority of the LSBRS is bordered by pastures for cattle, and in recent years some forest fragments at the site have been reduced in size on land not owned by the LSBFS (AL, pers. obs.; Pruetz and Leason, 2002). This region of Costa Rica averages 3,962 mm of rainfall per year, with a mild dry season between January and May (Sanford et al., 1994). Three primate species inhabit the area: the black-handed spider monkey (*Ateles geoffroyi*), the white-faced capuchin (*Cebus capucinus*), and the mantled howler monkey (*Alouatta palliata*).

I observed the positional behavior of the mantled howler monkey in two forest fragments in the LSBFS (Fig. 1). The first fragment, the aptly-named Small Forest, is

a primary forest fragment of approximately 12 ha that was selectively logged in the 1970s (Bezanson, 2006; Pruetz and Leason, 2002; Garber and Rehg, 1999). In the late 1990s, the fragment was 15-20 ha, but it has decreased in size from 1999 to the present (Pruetz and Leason, 2002; Garber and Rehg, 1999). Although all of the forest fragments at the LSBFS are characterized by a degree of anthropogenic disturbance, the Small Forest represents the least disturbed habitat at the site. The other fragment, the Large Forest, consists of approximately 30



**Figure 1.** Map of La Suerte Biological Field Station, Costa Rica. 1 – Small Forest, 2 – Large Forest, 3 – Logged Forest, 4 – Undescribed Forest Fragment. From Pruetz and Leason (2002).

ha of secondary forest, although the fragment is actually much larger, with an additional 70 ha of forest on property adjacent to the LSBFS (Pruetz and Leason, 2002). Trees are generally smaller and farther apart in the Large Forest, and the canopy is highly discontinuous. These fragments are connected by a thin corridor of riparian forest along the La Suerte River, which runs through both areas.

Researchers studied the positional behavior and habitat use of four groups of mantled howler monkeys, with 9-15 individuals in each group, in August 2010. Two of these groups inhabited the Small Forest, while the other two had home ranges within the Large Forest exclusively. I observed a fifth group within the corridor between the two forest fragments, but the study groups did not travel between the two areas. All of the groups were fully habituated from the beginning of the study, as the LSBFS functions as a dedicated research center and field school for university students throughout the year.

We recorded locomotor and postural behavior, as well as habitat utilization, using instantaneous observation on a focal animal at five minute intervals. Four observers made observations from 6am to 6pm each day, following groups from rising at dawn to bedding down at dusk. Observers split in to two teams each morning, allowing the observation of two groups per day. Within each group, observers chose one male and one female as focal animals each morning and followed these animals for the entire day. If an individual could not be followed for more than three consecutive intervals (15 minutes), the researcher chose another animal of the same sex to observe. Switching focal animals was usually unnecessary, particularly due to unique color patterns and facial scars that were helpful in differentiating between individuals. A five minute interval is more conservative than more frequent observations, helping to ensure temporal independence between samples. Despite this measure, we cannot assume that there is



complete independence between samples, as behaviors can be dependent upon others even over five minute intervals.

At each interval, we recorded the following data, based partially on variables established by Gebo (1992): activity (feeding, movement, or rest), posture/locomotion type (quadrupedal, bridging, climbing, suspension, quadrupedal suspension, clinging, curled, prone, sitting), forest stratum (ground, understory = between ground and 5 m, lower canopy = between 5 and 10 m, upper canopy = between 10 and 25 m, emergent layer = greater than 25 m), support size based on circumference (small = less than 5 cm, medium = between 6 and 25 cm, large = over 25 cm), and support orientation (horizontal = within 15 degrees of the horizontal, vertical = within 15 degrees of the vertical, oblique = between 15 to 75 degrees from the horizontal) (Table 1).

Several studies have indicated that the effect of habitat structure on primate positional behavior is complex, and that individual species, including howler monkeys, may adapt to their habitats in unique ways (Gebo and Chapman, 1995a; Gebo and Chapman, 1995b; Gebo, 1992; Wheeler and Ungar, 2001; Garber, 2007). As such, my research hypothesis is that the stratum use, support use, and positional behavior of *A. palliata* will differ between the primary and secondary forest sites studied. Due to the large numbers of variables involved in analyses of positional behavior, as well as the difficulty in assuming sample independence and normality due to temporal relations between behaviors, nonparametric statistical testing must be used for these data. I used a Mann-Whitney U nonparametric test for two independent samples to analyze the data, with a significance level of  $P < 0.05$ . I calculated frequencies of stratum use, support use, and positional behavior for each day that individuals were observed in each forest. These data in stratum use, support use, and positional behavior were compared between the Large Forest and Small Forest.

**Table 1.** Variables**Positional Behavior**

Quadrupedalism – movement in which all four limbs move regularly on a horizontal or oblique support, including walking and running

Bridging – movement in which gaps are crossed by body stretching, with the hindlimbs grasping an initial support and the forelimbs reaching for a distant one

Climbing – vertical movement in which the forelimbs pull and the hindlimbs push the animal up

Suspension – posture in which the body of the animal is suspended under a support by limbs and/or tail

Quadrupedal Suspension – movement in which all four limbs are used while suspended beneath a support

Clinging – posture in which the animal clings to a vertical support without sitting on another support

Curled – posture in which the animal rests with all four limbs partially abducted

Prone – posture in which the animal rests with all four limbs completely abducted

Sitting – posture in which the animal rests on its haunches

**Forest Strata**

Emergent – greater than 25 meters

Upper Canopy – 10 to 25 meters

Lower Canopy – 5 to 10 meters

Understory – less than five meters

Ground

**Support Sizes**

Large Support – more than 25 centimeters in circumference

Medium Support – between 6 and 25 centimeters in circumference

Small Support – less than or equal to 5 centimeters in circumference

**Support Orientation**

Vertical – within 15 degrees of the vertical

Horizontal – within 15 degrees of the horizontal

Oblique – between 15 to 75 degrees from the horizontal

**3. Results****Positional Behavior**

There were no significant differences in habitat use or positional behavior frequencies between howler monkeys in each study site (Table 2). The null hypothesis was retained in each statistical test. The most common postures and locomotor behaviors were sitting (41% of recorded activities in the Small Forest, 28% in the Large Forest,  $U = 13$ ,  $P > 0.05$ ), followed by quadrupedal walking (32% and 31%,  $U = 9$ ,  $P > 0.05$ ), suspension (16% and 26%,  $U = 4$ ,  $P > 0.05$ ), clinging (7% and 8%,  $U = 10$ ,  $P > 0.05$ ), and bridging (2% and 3%,  $U = 10$ ,  $P > 0.05$ ), in that order. Prone postures, climbing, curled postures, and quadrupedal suspension were

uncommon, but frequencies of these activities remained nearly identical between study groups ( $U = 6$ ,  $P > 0.05$ ;  $U = 10$ ,  $P > 0.05$ ;  $U = 7.5$ ,  $P > 0.05$ ;  $U = 7.5$ ,  $P > 0.05$ , respectively). Overall, the mantled howler monkey locomotor repertoire is centered on quadrupedalism and bridging. Sitting and suspension were the predominant feeding postures.

**Table 2.** Percentages and ranked order of positional behaviors during feeding and movement\*

Positional Behavior	Small Forest		Large Forest	
	%	Rank	%	Rank
Sitting	40.5	1	27.8	2
Quadrupedalism	31.6	2	31.1	1
Suspension	16.4	3	26.1	3
Clinging	6.7	4	7.8	4
Bridging	1.9	5	3.3	5
Prone	0.5	6	2.8	6
Climbing	0.2	8	0.6	7.5
Curled	0.2	8	0.6	7.5
Quadrupedal Suspension	0.2	8	0	9

\*Data from Small Forest are based on 402 records of positional behavior. Data from the Large Forest are based on 180 records of positional behavior.

## Support Use

Support sizes and orientations used in each study site were, again, indistinguishable (Table 3). There was a clear preference for small supports, which were used in 62% of recorded activities in the Small Forest, and in 73% in the Large Forest ( $U = 3$ ,  $P > 0.05$ ). Medium supports were also used (35% and 21%,  $U = 14$ ,  $P > 0.05$ , respectively.) The monkeys rarely used large supports (4% and 3%,  $U = 12$ ,  $P > 0.05$ ). Support orientations preferred were similarly skewed. In the Small Forest, 73% of activities took place on horizontal supports. The frequency in the Large Forest was similar, at 66% ( $U = 11$ ,  $P > 0.05$ ). Oblique supports were the second most common in each study site, with 23% and 26% of observations ( $U = 5.5$ ,  $P > 0.05$ ). Vertical supports were very rarely used (6% and 9%,  $U = 7$ ,  $P > 0.05$ ); this is congruent with the

monkeys' emphasis of quadrupedal walking and suspension, and low frequencies of climbing behavior.

**Table 3.** Percentages and ranked order of arboreal supports used during feeding and movement\*

Support Size	Small Forest		Large Forest	
	%	Rank	%	Rank
Small	62	1	73.3	1
Medium	35.4	2	21.7	2
Large	4.3	3	2.8	3
Support Orientation				
	%	Rank	%	Rank
Horizontal	72.9	1	65.6	1
Oblique	22.8	2	25.6	2
Vertical	6.1	3	8.9	3

\*Data from Small Forest are based on 402 records of positional behavior. Data from the Large Forest are based on 180 records of positional behavior.

### Forest Strata Use

Although the differences were not statistically significant, there were differences in rank order in forest strata usage (Table 4). In the Small Forest, the upper canopy was the most commonly used forest layer, with 65% of observations occurring within it ( $U = 11$ ,  $P > 0.05$ ). The lower canopy was the second most highly used layer in that study area, with 23% of observations ( $U = 2$ ,  $P > 0.05$ ), followed by the emergent layer (11%,  $U = 11$ ,  $P > 0.05$ ). Usage of the understory was negligible, and observations on the ground were nonexistent. In the Large Forest, this pattern differs slightly: the lower canopy is the most highly used layer (48%), followed by the upper canopy (44%), and emergent (8%).

**Table 4.** Percentages and ranked order of forest strata used during feeding and movement\*

Strata	Small Forest		Large Forest	
	%	Rank	%	Rank
Upper Canopy	65.1	1	43.9	2
Lower Canopy	23	2	48.3	1
Emergent	11.4	3	7.8	3
Understory	1	4	0	4

\*Data from Small Forest are based on 402 records of positional behavior. Data from the Large Forest are based on 180 records of positional behavior.

## 4. Discussion

### Methodological Limits

Several methodological factors may have limited the results and analysis of this study. Temporally, the study was limited to the wet season, which may have implications for positional variability. A lack of distinction between travelling and foraging behaviors may have influenced the data. Finally, the study sites may not have been distinctive enough to accurately reflect the influence of forest structure on positional behavior.

### Temporal Influence

The relationship of seasonality to primate positional behavior is poorly understood, and the results of a number of previous studies have been mixed. In a study of red colobus monkeys (*Piliocolobus badius*), Gebo and Chapman (1995a) found little evidence of seasonal effects on positional behavior, and recorded more differences annually than seasonally. The only exception—and the only statistically significant difference found—was a 21% decrease in quadrupedal locomotion in the wet season during foraging. Although this was a sizeable difference, the authors concluded that seasonal effects were minimal, and what variation did occur did so during foraging rather than travelling. The authors also noted that when comparing different seasons in different years (the wet season of 1990 and the dry season of 1991), the

difference in quadrupedalism decreased from 21% to only 5%, suggesting that annual variation may be more pronounced than seasonal differences.

Dagosto (1995), observing four sympatric species of Malagasy primates (*Propithecus diadema*, *Eulemur fulvus rufus*, *Eulemur rubriventer*, and *Varecia variegata*), observed significantly more variation, but likewise found that differences in travelling behavior were relatively conservative, while variation during foraging was more pronounced. In the three lemurid species observed, leaping occurred significantly more in the dry season than in the wet season, while the opposite was true of quadrupedalism. Support use, however, was highly consistent seasonally. In contrast, in *Propithecus diadema*, the diademed sifaka, support use differed seasonally, while positional behavior did not. Seasonal variability appears to be most pronounced during foraging behavior. Garber suggests that this pattern “may be associated with seasonal changes in diet, foraging strategies, and the availability and distribution of feeding sites” (2007: 555). However, differences between sympatric species of different families demonstrate the difficulty in predicting such broad patterns.

Research on the red howler monkey (*Alouatta seniculus*) complicates the picture further (Youlatos, 1998). In red howlers, there is significant seasonal variation during travelling behaviors, and little variation during foraging; the complete opposite of the generally observed pattern. During the dry season, Youlatos observed increased use of the emergent layer during travelling, as well as an increase in leaping and quadrupedalism. These results further emphasize the difficulty in uncovering broad patterns of seasonality and positional behavior. Amounts of variation appear to differ wildly between taxa, and certain taxa appear to display trends that completely contradict the trends observed in others. My study took place entirely in the wet

season, and it is possible that the results could have differed significantly over a longer temporal span.

### **Travel and Foraging**

Many authors have observed that foraging and travelling behaviors are associated with significantly different locomotor patterns. Foraging may be defined as movement within a centralized feeding area (generally a single tree or group of trees) without a particular group direction. Travelling implies group direction of movement, and takes place over longer distances. The exact patterns exhibited appear to differ between species, making broad characterizations difficult. Dagosto (1995) notes that among many species of lemurs, Old World monkeys, and New World monkeys, frequencies of leaping decrease during foraging, while climbing and quadrupedalism become more common. This observation appears to hold true for a wide range of arboreal quadrupeds (Gebo, 1991; Gebo and Chapman, 1995a; Dagosto, 1995; McGraw, 1998; Bitty and McGraw, 2007). Perhaps unsurprisingly, in more highly specialized arboreal primates, such as *Propithecus diadema*, a dedicated leaper, the same pattern is not present, and in fact there are no significant locomotor differences between foraging and travelling (Dagosto, 1995).

As highly generalized arboreal quadrupeds, mantled howler monkeys (*Alouatta palliata*) align with the pattern quite closely, with a few additions. During travel, quadrupedalism is most common, followed by climbing, then bridging, then leaping (Gebo, 1992; Johnson and Shapiro, 1998). During foraging, climbing frequencies increase while quadrupedalism and leaping decrease in a way similar to many other arboreal quadruped taxa. In addition, mantled howlers demonstrate increased quadrupedal suspension during foraging, while bridging frequencies decrease (Gebo, 1992). As a slow, deliberate arboreal quadruped that emphasizes bridging and

suspension and rarely leaps, these differences from the common model are unsurprising in regards to howlers. Differences in posture and habitat use are also clear between travelling and foraging. During foraging, suspensory postures are much more common, small and oblique supports are used heavily, and the monkeys prefer the lower canopy. During travel, mantled howlers prefer medium and large horizontal supports in the upper canopy (Gebo, 1992).

In this study, I did not distinguish between foraging and travelling. Due to the lack of such a distinction, data in posture use, support use, and forest strata use may have been skewed in unpredictable ways depending on the ratios of foraging to travelling as the monkeys were observed. As positional behavior variation tends to be much more conservative in travel than in foraging, it is possible that by isolating instances of foraging within this dataset, significantly more variation would have become apparent.

### **Distinction between Forest Types**

An assumption inherent to this research is that the two study sites at La Suerte, the Small Forest and Large Forest, are structurally distinct. Various researchers working at La Suerte have described the study areas in terms with subtle differences, making the structural distinctness of each site somewhat questionable.

The Large Forest is a 30 ha area within a 70 ha forest fragment. Selectively logged in the 1970s, the fragment is generally considered to be secondary forest. However, it has also been characterized as advanced secondary forest, implying that the forest has recovered from anthropogenic disturbance to a large degree and is somewhat intermediary between primary and secondary forest (Bezanson, 2006; Bezanson, 2009). The actual status of the Small Forest is equally unclear in the literature. In studies in the 1990s, the area, which also saw some selective logging in the 1970s, though to a lesser degree than the Large Forest, was identified as advanced



secondary forest itself (Garber and Paciulli, 1997; Garber and Rehg, 1999). This characterization has been cited into the 2000s (Pruetz and Leason, 2002). However, more recent studies have identified the fragment as primary forest (Bezanson, 2006; Bezanson, 2009).

It is likely that over the past twenty years, both fragments have continued to recover, prompting the most recent studies to classify the Small Forest as primary and the Large Forest as advanced secondary. Regardless of which classification is followed, however, a key element of the relationship between the forests is that one is advanced secondary forest while the other is either primary or secondary. If this is the case, the two sites may simply not be distinct enough to reflect positional behavior variation in the way that a comparison of two more disparate forests, such as the dry forest as Santa Rosa, Costa Rica, and the wet forest as La Suerte, for example, might (Garber, 2007). Unfortunately, detailed structural analyses of the study sites at La Suerte are not available. However, based on surveys conducted by students of the Field School over the last several years, the areas do appear to be structurally distinct: in the Large Forest, trees tend to be significantly smaller and farther apart, and the canopy is discontinuous (G. Donati, *personal communication*).

## **Other Studies**

A number of studies have documented the positional behavior of the mantled howler monkey, and my results align with these fairly closely (Mendel, 1976; Gebo, 1992; Johnson and Shapiro, 1998; Bezanson, 2009) (Table 5). In every study, sitting is the most common feeding posture used by the species. Suspension is the second most common feeding posture, comprising 20-25% of feeding observations between studies. Similarly, quadrupedalism is the most common locomotor mode in each study. Some differences do arise in less common locomotor modes: Gebo (1992) attributes as many as 37% of locomotor bouts to climbing, while other studies

(Mendel, 1976; Johnson and Shapiro, 1998) observed climbing in only 9-11% of cases. As only 2% of observations by Gebo were recorded as vertical support use, it is likely that this high percentage of climbing recorded is due to a conflation of quadrupedalism on oblique supports with climbing. Bezanson (2009) represents another extreme, recording climbing in only 1% of cases. My own results are similar. 7.5% of my observations recorded clinging behavior, extremely rare in other studies. Other results, including bridging and leaping, closely aligned with other studies.

**Table 5.** Ranked order of positional behaviors across studies\*

Positional Behavior	Small Forest	Large Forest	Mendel (1976)	Gebo (1992)	Bezanson (2009)
Sitting	1	2	1	1	1
Quadrupedalism	2	1	2	2	3
Suspension	3	3	3	5	2
Clinging	4	4	N/A	N/A	5
Bridging	5	5	N/A	6	4
Prone	6	6	N/A	N/A	N/A
Climbing	8	7.5	4	3	5
Curled	8	7.5	N/A	N/A	N/A
Quadrupedal Suspension	8	9	N/A	7	5

\*Data from Small Forest are based on 402 records of positional behavior. Data from the Large Forest are based on 180 records of positional behavior.

Habitat usage recorded was also similar between studies. Support sizes observed fell within the ranges observed by Gebo (1992) and Bezanson (2009). Mendel (1976), despite a slight difference in variables, came to extremely similar results, with large supports accounting for approximately 3% of observations. Gebo recorded a preference for oblique supports, followed by horizontal, with vertical supports making up 2% of observations. My own observations differed slightly, with horizontal supports as the most commonly used, and vertical supports used more commonly, if still rarely (6-9%). Forest strata use was similar as well: although my variables differed from those of Gebo (1992) slightly, there was a clear preference

for the upper and lower canopy (upper and middle canopy in Gebo), with understory usage rare (lower canopy in Gebo), and no observed ground usage.

Observations by Youlatos (1998) on the red howler monkey (*Alouatta seniculus*) and Prates and Bicca-Marques (2008) on the black and gold howler (*Alouatta caraya*) were also similar to my own, with the exception of a few unusual behaviors by *A. caraya*. Prates and Bicca-Marques observed a group of 12-14 black and gold howlers in a 0.7 ha orchard forest at Estabelecimento Nossa Senhora da Conceicao, Brazil. The study site contained 7 native and 7 exotic plant species, and was dominated by orange trees. Several observations from the study are unusual. Suspensory postures made up a very low portion of feeding postures, approximately 4% (versus 15% in a group of *A. caraya* in primary wet forest). Quadrupedal locomotion was also fairly rare in the orchard forest, and was recorded half as often as in the control group. Climbing, descending, and leaping were much more prominent in the orchard group as well. Perhaps most strikingly, the animals descended to the forest floor for 4.4% of observations. The authors suggest that these distinctive locomotor patterns were the result of travel in the unique environment of the orchard forest, which was characterized by a highly discontinuous canopy. Such a reliance on leaping and even terrestrial locomotion over bridging in order to cross canopy gaps is rare in the mantled howler monkey, although *A. caraya* and *A. palliata* are similar in size, activity pattern, and positional behavior otherwise.

Overall, my results were similar to those of a number of other studies of *A. palliata*, and are comparable with the positional behavior of the species and the genus as a whole. Without data from a more diverse array of mantled howler habitats, it is difficult to analyze site-specific intraspecific variation through cross-study comparisons. However, the unique positional behavior pattern observed in *A. caraya* in an orchard forest in Brazil and the seasonal variation

recorded in *A. seniculus* by Youlatos (1998) support the hypothesis that *Alouatta spp.* positional behavior is influenced by habitat characteristics.

### **Previous Discussion of Intraspecific Variation in *Alouatta***

The influence of habitat structure on primate positional behavior has been the subject of some debate, and research on howler monkeys on this topic is lacking (Dagosto, 1995; Garber and Pruetz, 1995; Garber, 1998; McGraw, 2000). Due to a lack of uniformity in variables and methods, cross-study comparisons of positional behavior are difficult (McGraw, 2000).

Nevertheless, Garber and Pruetz (1995) have suggested that intraspecific variation is likely in mantled howler monkeys based on studies in Barro Colorado Island, Panama (Mendel, 1976) and Hacienda La Pacifica, Costa Rica (Gebo, 1992). The authors note that between-site positional behavior variation appears to be present on a species-specific basis, and it is worth noting that this variance appears to be more common in relatively large-bodied arboreal quadrupeds, such as *Alouatta spp.*, than in smaller-bodied animals, or in species with more specialized locomotor patterns (Garber and Pruetz, 1995; Gebo and Chapman, 1995a; Dagosto and Yamashita, 1998).

In the case of the howlers in Barro Colorado and La Pacifica, Garber and Pruetz suggest that climbing and bridging behaviors were significantly more common “in the drier Costa Rican forest” than in Panama (1995: 424). Gebo (1992) reports climbing in 37% of observations, and bridging in 10%. Mendel (1976), in contrast, reports only 9% climbing and no bridging behavior. The large disparity in climbing may be related to differences in methodology. The definitions of climbing used by each author differ significantly. Mendel describes climbing as “locomotion on substrate greater than 60° from the horizontal” (1976: 37-38). Gebo’s definition is more qualitative:

movements which require greater mobility in the limbs; a movement up or down a vertical or steeply incline support or through irregular and intertwined small supports; all four limbs move in an often irregular pattern with adducted arms and knees and with variable hand and foot positions; the arms are used to pull the animal while the legs alternately push the body upward/forward. (1992: 279).

Mendel's declaration that climbing occurs only on substrates at  $60^\circ$  from the horizontal or greater refers to locomotion occurring on substrates that Gebo classifies as vertical ("from 75 to 105 degrees of the vertical") and the upper limits of oblique ("between 15 and 75 degrees from the horizontal") (1992: 279). As both authors agree that vertical support use is rare, it is likely that some activity qualitatively described as climbing on both oblique and vertical supports by Gebo may have been characterized by Mendel as quadrupedalism because it took place on supports less than  $60^\circ$  from the horizontal (1976; 1992). It is also worth noting that Mendel reported quadrupedal walking in 70% of observations, while Gebo did so in only 47%. The difference in these measurements, perhaps coincidentally, corresponds closely with the difference in reported frequencies of climbing.

The lack of bridging behavior reported by Mendel (1976) is puzzling. The behavior—an important gap crossing mechanism in a species that does not regularly leap—is relatively common in mantled howlers as well as other members of the genus, and has been widely documented (Gebo, 1992; Youlatos, 1993, 1998; Bezanson, 2006, 2009). Sampling methodologies used by Mendel and Gebo were fairly similar: Mendel performed instantaneous sampling on a focal animal at five second intervals, while Gebo used continuous sampling of a focal animal (Mendel, 1976; Gebo, 1992). Although instantaneous and continuous methods are quite different, Mendel's interval time was quite short (intervals from one to five minutes are

more common), and would be functionally similar to continuous methods. Mendel does note several issues that may have been related to these locomotor observations (1976). Due to difficulties keeping focal animals under constant surveillance for a large portion of locomotor observations, locomotor modes were only recorded for 2% of focal animal observations. As such, Mendel recommends that the locomotor data presented “be regarded only as an estimate and not well established by large, independent samples” (1976: 42).

These issues demonstrate the difficulty of such cross-study comparisons. Without uniformity in variables, methodology, and habitat quantification, the usefulness of cross-study comparisons of positional behavior is quite limited (Hunt et al., 1996; McGraw, 2000). In the case of *A. palliata*, further positional behavior research using the same methodology in highly distinct habitat types is necessary to evaluate the question satisfactorily.

### **Positive Implications**

The relative resilience of howlers to anthropogenic disturbance has been noted for some time. Arroyo-Rodríguez and Dias (2009) claim that three of the four main causes of the global decline of primate populations are anthropogenic in nature: hunting, habitat conversion, and habitat fragmentation. Howlers are relatively successful in disturbed and fragmented habitats, and often exist in areas in which other Neotropical primates do not (Arroyo-Rodríguez and Dias, 2009). This trait is likely related to their relatively generalized, folivorous diet, which is not dependent upon patchily distributed food sources which may be difficult to obtain in disturbed and fragmented forests. In cases of high population density due to small fragment size, howlers increase the diversity of their diets, consuming novel and low-quality food items. In addition, plant species associated with disturbed habitat represent a large portion of the howler diet (Cristóbal-Azkarate and Arroyo-Rodríguez, 2007).

Nevertheless, the threats of habitat disturbance and fragmentation are quite real for howlers. As highly arboreal animals dependent on a relatively continuous canopy, travelling between forest fragments is difficult and dangerous for howlers. This is especially true when fragments are separated by croplands or pastures for cattle, as is often the case in Costa Rica, and is particularly evident at La Suerte (Arroyo-Rodríguez and Dias, 2009). In these cases, howlers are particularly vulnerable to hunting and predation. Although these animals cope with habitat change well, disease, predation, parasitism, and risks of increased competition with other species also increase in disturbed habitats. As a result of habitat loss likely related to anthropogenic disturbance, two subspecies of *A. palliata*, *A. palliata aequatorialis* and *A. palliata mexicana*, have been declared vulnerable and critically endangered, respectively, by the International Union for the Conservation of Nature (Arroyo-Rodríguez and Dias, 2009).

The results of this study may have positive implications for conservation of mantled howlers living in anthropogenically disturbed habitat. The Large Forest and Small Forest fragments at La Suerte have both been disturbed by logging as recently as the 1970s. The effects of this activity have been much more pronounced in the Large Forest than in the Small. Despite these differences, mantled howlers living in each fragment appear to display nearly identical patterns of positional behavior, reflecting a pattern of behavioral resilience rather than flexibility. As noted previously, howlers living in disturbed habitats tend to differ in terms of diet from those living in pristine habitats, specializing in secondary plant species and broadening the variety of items ingested (Cristóbal-Azkarate and Arroyo-Rodríguez, 2007). In terms of locomotor behavior, such a trend toward flexibility and adaptability is not apparent. Instead, the positional behavior repertoire of the species appears to be unaffected by some degree of environmental disturbance, despite significant differences in forest composition including a

discontinuous canopy and differences in available substrates and food distribution. The species represents a resilient pattern in which they are able to interact with distinct environments in similar ways, likely due to their highly generalized dietary and locomotor adaptations.

As evidenced by the highly distinctive locomotor behaviors exhibited in black and gold howlers at Estabelecimento Nossa Senhora da Conceicao, Brazil (see above) environmental disturbance to great degrees has a clear effect on howler positional behavior (Prates and Bicca-Marques, 2008). However, the highly pronounced disturbance characteristic of an orchard forest is not likely in a recovering secondary forest fragment. As such, howlers are likely capable of thriving even in relatively disturbed habitats, which is a hopeful sign for members of the species (and likely genus) living in recovering forests. Regardless of their ability to persist in disturbed habitat, however, howlers do still face danger from habitat fragmentation. Both forest fragments at La Suerte have decreased in size steadily over the past 30 years. This trend is unfortunately common in forest fragments bordered by farm and grazing land, despite their protection from current direct anthropogenic pressures such as logging. Howlers lack the ability to easily migrate between fragments, and as such care must be taken to preserve large fragments as much as possible and to increase the size of small and medium-sized ones.

### **Future Research**

Further research on mantled howler positional behavior in a number of highly distinct habitat types is clearly necessary. *A. palliata* inhabits a wide geographic range throughout the neotropics, and free-ranging groups have been observed in a number of habitat types throughout this range, including primary and secondary wet forest, dry forest, riparian forest, and orchard forest (Mendel, 1976; Jones, 1980; Gebo, 1992). Unusual variation in positional behavior has been observed in the closely related species *A. caraya*, making them another useful study species



(Prates and Bicca-Marques, 2008). Through the use of a standardized methodology, variables, and detailed quantitative analysis of habitat types, research of *A. palliata* positional behavior at a number of highly distinct study sites may reveal interesting patterns regarding intraspecific variation within the species and within arboreal quadrupedal primates as a group. Such a detailed analysis may shed light on the effects of individual habitat characteristics on positional behavior. Analysis of quantifiable habitat types may prove useful for understanding the complexities of extinct primate locomotion and evolution, and may provide valuable insights for the conservation of extant species.

A heavy use of video-recording in such a future study may be particularly beneficial. By recording primate positional behavior and analyzing the videos to obtain data at a later time, a researcher can gather highly complex data, free from the constraints of traditional ethological data collection. Through an analysis of recorded video, it is possible to collect highly accurate and highly complex data on as many animals as were recorded at any one time. The process is more time consuming than traditional methods, but the high degree of accuracy, complexity, and detail available would prove useful for both qualitative and quantitative analysis. In addition, such recordings could be used for research in other related subjects, as well as for multimedia presentations, teaching, and conservation outreach.

## **5. Conclusion**

I observed the positional behavior of the mantled howler monkey, *Alouatta palliata*, in two forest fragments in northeastern Costa Rica. In order to determine the effects of habitat structure on positional behavior and to analyze the range of variability within a species, I compared data collected from groups in primary and secondary wet forest habitats. This information may allow us to understand and reconstruct the locomotion of extinct primate

species in greater detail. It may also allow us to better understand the ability of extant primates to cope with various levels of environmental degradation and the way in which primates utilize their environment for conservation and forest recovery efforts.

Despite several indicators that mantled howlers may exhibit intraspecific variation in positional behavior, I found no statistically significant differences in locomotion, posture, or habitat use between the two forests. These results may have been affected by several methodological issues, including a relatively short study period that did not account for seasonality or a lack of distinction between travelling and foraging behaviors during movement. In addition, it is possible that the two study sites were not significantly structurally distinct enough to analyze such variation. Despite these possible issues, the results were generally congruent with previous studies of mantled howler positional behavior. Unfortunately, cross-study comparisons of positional behavior are difficult due to a number of factors unless the methodology used was uniform. As such, I suggest a study of mantled howler locomotion using a standardized methodology, video-aided data collection, and a variety of highly distinct habitat types, in order to more thoroughly understand intraspecific positional behavior variation. Regardless, a lack of variation between disturbed and pristine habitats may have positive implications for conservation: mantled howler monkey positional behavior, which influences diet and activity pattern, appears to owe relatively little influence to environmental disturbance.

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